Part III: Habitats

Chapter 17

Vulnerability of coral reefs of the Great Barrier Reef to climate change

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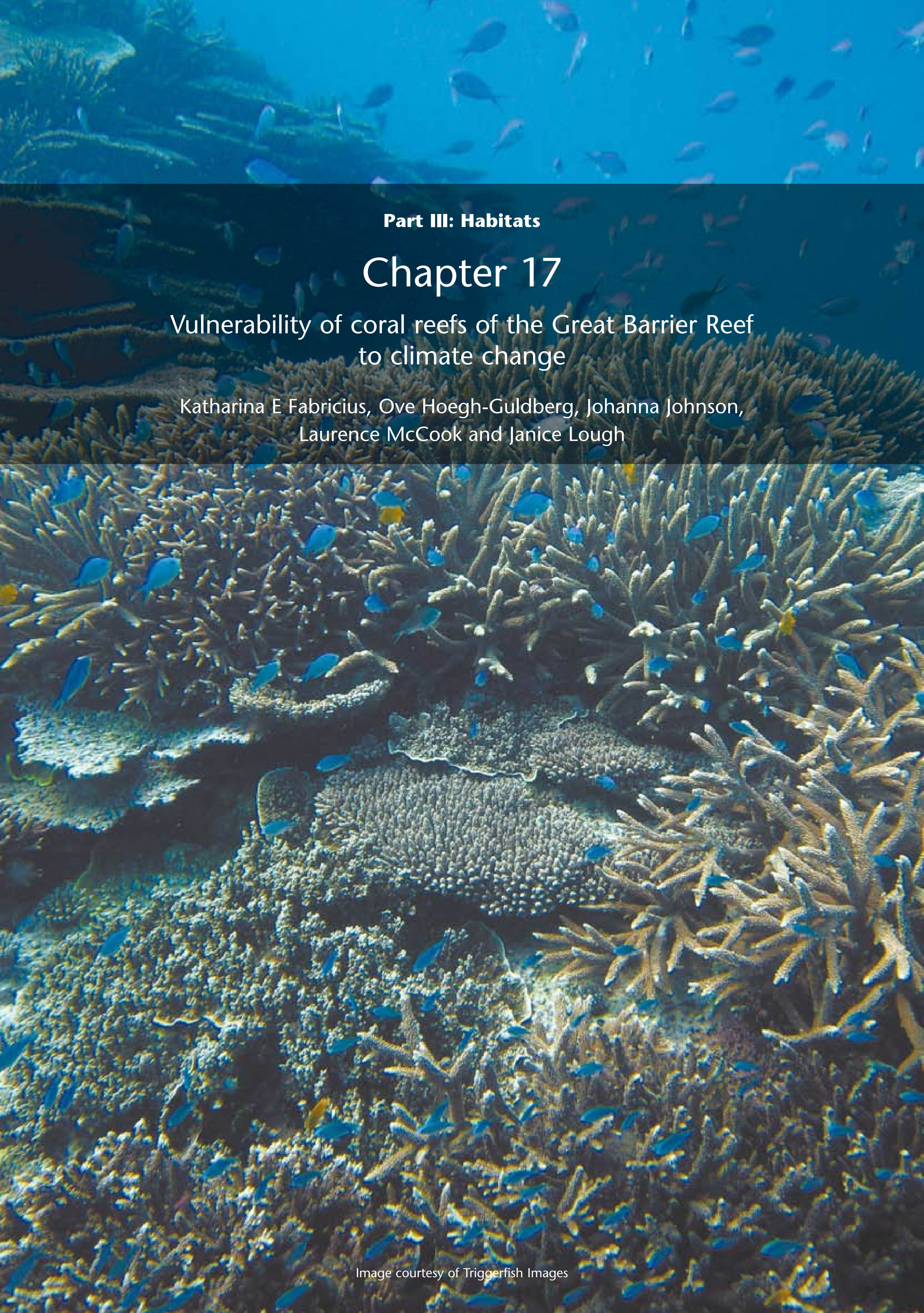

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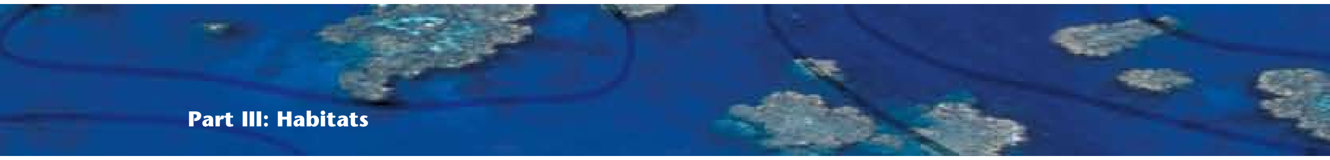

17.1 Introduction

The Great Barrier Reef (GBR) contains the most extensive coral reef ecosystem on earth. It consists of 2900 coral reefs and 900 coral cays that cover approximately 20,000 km^2 of the total 345,000 km^2 area of the GBR Marine Park. As a consequence of unusually high summer sea surface temperatures, between 42 to 60 percent of the reefs of the GBR experienced mass coral bleaching in 1998[8]. Bleaching was also reported from 31 other nations around the world during 1997–1998. For example, about 50 percent of reefs in the Indian Ocean and south Asia lost much of their coral cover, and an estimated 16 percent of the world's area of coral reefs was severely damaged[43]. The event coincided with the strongest recorded El Niño-Southern Oscillation event (ENSO) and one of the warmest years on record[78,106]. In early 2002, another mass bleaching event occurred on the GBR, exceeding the 1998 event in scale and severity[8]. Again, it was linked to record summer sea surface temperatures, despite weak ENSO activity[8]. These bleaching events alerted the world to the vulnerability of coral reefs to climate change. The responses of reef-building scleractinian corals are now much better understood than those of other groups of reef associated organisms[12,54,25] (Hoegh-Guldberg et al. chapter 10). This chapter reviews what is known of the vulnerability of GBR coral reefs to climate change at the ecosystem level. We consider how the ecosystem is affected by: i) increasing sea temperature, ii) irradiance, iii) ocean acidification, iv) frequency of intense tropical storms and v) altered rainfall and river flood plumes. The chapter focuses on the ramifications of increased coral mortality on ecosystem functions, including rates of calcification and erosion, reduced structural complexity and thus provision of habitat and shelter for reef-associated species. The chapter also considers the implications of significant loss of coral cover resulting in shifts in trophic structure and competitive advantages for some species within the ecosystem.

Assessing the vulnerability of GBR coral reefs at an ecosystem level is complicated due to the natural complexity of the system. The GBR ecosystem has a range and diversity of habitat types represented by over 70 distinct reef and non-reef bioregions identified based on their contrasting geophysical and biological characteristics[35]. These bioregions represent a gradient from tropical to subtropical reefs (between 12 to 24 °S), and across the continental shelf from turbid and shallow coastal reefs to reefs in deep blue-water oceanic environments. Additionally, extensive submerged coral reefs, coral communities and coral-associated organisms occupy parts of the deep seafloor. The GBR has high biodiversity and complex interactions, which all contribute to a greater or lesser extent to shaping the ecosystem. The coral reefs of the GBR are formed by the calcium carbonate skeletons of over 400 species of hard corals, the carbonate deposits of a number of calcifying algae, foraminifera, molluscs, tube-forming annelid worms and octocorals, as well as abiotic carbonate precipitation. These complex carbonate structures form the habitat for many tens of thousands of species of protozoans, fungi, marine plants and animals. For example, more than 1000 species of marine plants, 1500 species of sponges, 4000 species of molluscs, 800 species of echinoderms and over 1500 species of fish have been recorded on the GBR to date, with new species being added every year. This high habitat and species diversity contributed to the listing of the GBR as a World Heritage Area in 1981. An assessment of the vulnerability of such a complex system, in which not all of the key processes are currently understood, will necessarily be simplistic and can only focus on a few of the processes and interactions that are presently better understood.

An assessment of the vulnerability of the GBR to climate change is important to better predict potential future changes and as a foundation to investigate and develop potential adaptation strategies. The contribution that all GBR industries (tourism, recreation and fisheries) make to the Australian economy has been estimated at A$6.9 billion (Australian dollars) per year[53,1]. Economic returns are generated from a highly profitable tourism industry, and smaller reef-related industry sectors such as commercial fisheries and recreational activities. Additional ecosystem services provided by reefs include coastal protection and the storage of libraries of bioactive substances being investigated for potential pharmaceutical benefit. The total annual economic value of coral reefs has been estimated at US$100,000 to 600,000 per square kilometre[115], although these values are probably underestimates as they only consider direct services and outputs. Due to their ecological and economic value, and amazing beauty, coral reefs are generally treated as the iconic habitat within the GBR.

17.2 Exposure and sensitivity to climate change and impacts on reefs

17.2.1 Sea surface temperature

17.2.1.1 Exposure

Sea temperature is a key factor for organisms associated with symbiotic dinoflagellates (zooxanthellae) or that have a narrow temperature tolerance range. Coral reefs grow in shallow areas with good light penetration where water temperature rarely declines below 18°C. Globally, coral reefs are, therefore largely restricted to tropical or subtropical waters (between 30 °N and 30 °S), and to coasts without regular upwelling of cool deep waters (as occurs along most western continental margins).

Tropical sea surface temperatures have risen in the past century by 0.5°C, which is largely attributable to increasing greenhouse gas concentrations in the atmosphere. This trend is expected to accelerate in the current century[59,60]. Regionally, patterns of exposure to such warming can be quite complex. Both long-term average baseline sea temperature and warming trends significantly differ along and across the GBR, and at local scales:

- The long-term mean annual sea temperature is 3°C higher in the far north than in the south of the GBR (Lough chapter 2).
- The mean increase in annual sea temperature to date has been greater in the south of the GBR (approximately 0.5°C warming at 24 °S) than in the far north (approximately 0.3°C warming at 12 °S).
- The difference between summer and winter sea temperature is greater in the southern GBR (6°C seasonal change) than in the far northern GBR (seasonal difference: 4°C due to the moderating effects of more frequent shading by clouds and warm winters in the north).
- The difference between summer and winter sea temperature is greater in shallower inshore waters of the GBR compared with offshore waters, as inshore sea temperature is more than 1°C warmer in summer and generally cooler in winter.
- At smaller scales, significant localised warming is often encountered in semi-enclosed bays and cooling from upwelling may occur in some offshore sections.

Major large-scale thermal stress events tend to coincide with periods that may include extremely low wind, low tidal amplitudes, low turbidity, high irradiance and clear skies[41,12], resulting in minimal wave-induced flow, minimal shading by clouds and reduced backscatter after particles settled. The build-up of such heating conditions is particularly critical during times when baseline temperatures are already high. Relief comes from wind or tidally induced currents that reduce thermo-stratification in the water, and break up the boundary layers over the benthos surface, or from clouds that reduce solar heating[109,85]. Light exacerbates the effect of temperature.

Organisms on a coral reef will experience even greater fluctuations in water temperature than the long-term averages suggest. For example, *in situ* observations at an Australian Institute of Marine Science (AIMS) automatic weather station[a] on Myrmidon Reef indicate a seasonal variation of average daily sea temperatures of about 5°C while differences between observed daily maximum and minimum sea temperatures are 9 to 10°C (Lough chapter 2). Marine organisms have adapted to their thermal environment to exist between the high and low extremes as much as the mean sea temperature. In addition to the direct influence of sea temperature, the thermal environment of some organisms may be influenced by the absorptive properties of their colony or body surfaces. While sea temperature is a good predictor for the former, the latter is affected by temperature as well as irradiance, water flow and surface colour. Colony surface temperatures in darkly pigmented corals, for example, can be greater than 1.5°C warmer than ambient water temperatures at high irradiance and low currents[31].

Episodically, organisms are exposed to summer sea temperatures that lead to physiological stress or even mortality if thermal tolerance limits are exceeded. For example, in 1998 and 2002 on the GBR, about 42 and 54 percent of reefs bleached respectively, and up to 5 percent were severely damaged in each event[b]. There was considerable heterogeneity in the extent of bleaching between reefs of the GBR. Such heterogeneity can be linked to climate, weather, spatial and oceanographic factors that contribute to determining local and regional temperature exposure. These factors, and measures to assess exposure, are summarised in Table 17.1.

17.2.1.2 Sensitivity

Coral reefs grow and survive in a narrow range of environmental conditions and are therefore particularly sensitive to small changes in sea temperature. The sensitivity of ecosystem properties such as calcification and productivity is inevitably derived from the sensitivity of species groups such as corals and plankton. Chapters 5 to 16 in this volume summarise what is known about the sensitivity of other taxonomic groups. A key message is that taxa associated with endosymbiotic algae have particularly narrow upper and lower temperature tolerance ranges, while other groups can survive at much higher temperatures (eg seven species of tropical seagrasses at 40 to 45ºC for short periods[14]).

A diverse range of invertebrates is associated with endosymbiotic dinoflagellates, including many anthozoans (eg hard corals, anemones, zoanthids and octocorals), some sessile and pelagic hydrozoans (eg fire coral *Millepora* and some jelly fish), molluscs (eg the giant clam *Tridacna*,

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[a] http://www.aims.gov.au/pages/facilities/weather-stations/weather-index.html

[b] http://www.gbrmpa.gov.au/corp_site/info_services/science/climate_change

Table 17.1 *Factors that affect the exposure of coral reefs to sea surface temperature, reef sensitivity and potential impacts*

Exposure	Factors determining sensitivity	Potential and observed impacts
Factors determining exposure: • Latitude • Cross-shelf position • Small-scale features (embayments, channels) • Depth (thermal stratification in bays) • Currents, waves, tides and wind facilitating mixing and gas exchange, preventing thermo-stratification and surface heating • Upwelling of cool deep water bodies decreasing exposure • Cloud cover • Boundary layer conditions **Measures to quantify exposure:** • Mean summer sea temperature • Long-term seasonal change in mean and maximum sea temperature • Three-day maximum sea temperature • Degree heating weeks (intensity and length of exposure) • Turbidity • Flow and other factors that determine heat flux	• Species-specific phenotypic plasticity in temperature tolerance • Prior physiological stress (eg from low salinity, high nutrients) • Mobility • Association with endosymbiotic algae • Exposure history (eg exposure to high light and temperature) • Community composition	**Rise in mean annual water temperature:** • Accelerated metabolism, enhanced primary production, calcification, growth up to a threshold; declining rates thereafter due to heat stress • Lower water column productivity, less food for filter and plankton feeders, altered food webs and reef productivity • Altered reproductive timing (eg desynchronisation of spawning, shifted breeding season) • Range extension towards the south of heat sensitive species • Shifts in relative abundances of temperature tolerant versus sensitive species • More diseases **Increased frequency and severity of extreme temperature events:** • Damaged photosystems in primary producers • Corals: bleaching and increased mortality; lower reproductive output, reduced cover, lower structural complexity, lower reef calcification • Coral-associated organisms: less shelter and habitat due to low structural complexity • Facultative coral symbionts or epibionts: local extinction of highly specialised species (eg coral-associated gobies) • Fish: shifts in distribution, shifts in life history traits • Macroalgae: higher abundances (more substratum available, less shelter for herbivorous fish) • Internal bioerosion: more dead coral available as substratum for bioeroding organisms, resulting in reduced structural strength • Overall: reduced reef biodiversity, shift from net calcification towards net erosion, dominance by macroalgae

and some nudibranchs), and flatworms (Platyhelminthes). For these species, conditions become uninhabitable if temperatures drop below 16 to 18°C for more than a few weeks per year, or if they increase by 1 to 2°C above long-term maxima for days to weeks. The latter damages the photosystem II in the dinoflagellate, disrupting the symbiosis between endosymbiotic dinoflagellates and host, and causing the host to 'bleach'[119]. In corals, bleaching tends to occur when seasonal maximum sea temperatures at that location are exceeded by 4-degree heating weeks (equivalent to four week of exposure to temperatures 1°C above the long-term summer maxima; Hoegh-Guldberg et al. chapter 10). However, this threshold is a coarse average across species and locations, as bleaching sensitivity greatly varies between host taxa, and (to a lesser extent) between the genetic varieties of zooxanthellae they harbour[79,74] (Hoegh-Guldberg et al. chapter 10).

The sensitivity of species to sea temperature varies spatially and temporally. Temperature tolerance is higher in communities that have developed in naturally warm waters, such as the far northern GBR, the Persian Gulf or local areas such as poorly flushed bays, than communities of cooler regions[7,33]. For example, some corals with prior exposure to high temperature or high irradiance on intertidal reef flats regularly exposed to low tides and high temperature variability have also been found to be less sensitive to heat exposure, either through local selection or possibly through acclimation[13]. Similarly, whether the reproductive output of reef fishes is affected by increased sea temperature depends on whether they reside in locations close to their thermal tolerance limits for reproduction. Some species from predominantly temperate water fish families (eg *Pagrus auratus:* Sparidae) already appear to be at their thermal limit for reproduction in tropical water[105] and their populations on the GBR may decline as sea temperatures increase.

For most species groups and ecological processes on reefs, relative sensitivity to heat exposure and the mechanisms of temperature damage are still poorly understood. This is partly because of the high number of species that have not been studied, but also because field surveys of sensitivity are unavoidably biased by several factors. For example, the timing of surveys crucially influences results: a survey conducted soon after the onset of heat stress will result in high scores for sensitive coral species and low scores for more persistent species, whereas a survey conducted a few weeks later will show mostly persistent species in a stressed state, since the sensitive taxa will have already died and disintegrated[6]. Secondly, a community that has previously undergone a severe heat exposure will exhibit apparently low temperature sensitivity during the next heat exposure, if sensitive species have not yet re-established and the community consists of mostly persistent species.

17.2.1.3 Potential and observed impact

Rise in mean annual sea temperature

Water temperature is one of the most important variables determining ecosystem function in the marine environment. External temperature controls metabolic rates, which, during non-stress conditions, increase with increasing temperatures in all but warm-blooded organisms. Consequently, persistent warmer temperatures can accelerate life history and population parameters such as growth and reproductive age, and ecosystem properties such as rates of calcification and community metabolism, until they reach a level where temperature stress accumulates and rates start to decline[75].

While warmer sea temperatures increase growth rates in some organisms such as fleshy macroalgae, they may slow down growth in others because of the relative lower nutrient concentrations in warmer compared to cooler water. At higher temperatures, water column productivity accelerates, depleting the standing stock of dissolved and particulate nutrients including phyto- and zooplankton (McKinnon et al. chapter 6). For example, kelp and other temperate brown macroalgae grow most prolifically at cooler temperatures where nutrient concentrations are higher than in warmer nutrient-depleted waters[18], while the productivity of other macroalgae might increase at higher temperatures (Diaz-Pulido et al. chapter 7). Similar responses are likely to occur in other species groups, exemplifying that shifts in the relative abundances of species are to be expected, with profound but yet poorly understood consequences for ecosystem properties and species interactions.

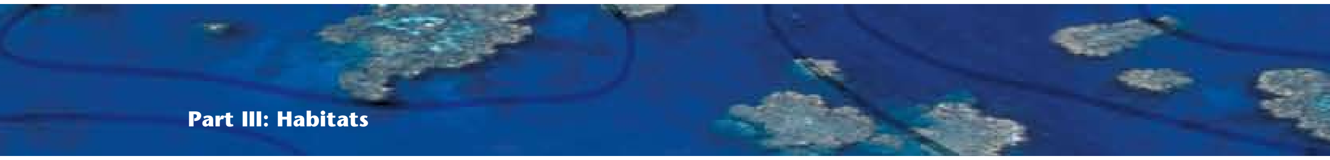
Altered reproductive timing has been linked to rising mean annual sea temperature. Of particular concern is a potential desynchronisation of the mass-spawning event of corals that occurs annually in the GBR. Thousands of coral species from unrelated taxa synchronise their annual spawning based on sea temperature and moon phase[5]. The role temperature plays is demonstrated at Magnetic Island off Townsville, where waters are approximately 1°C warmer than in the surrounding region and a proportion of species spawn one month earlier on this reef than conspecifics in cooler waters near-by. Similarly, reproduction of fishes on the GBR appears to be triggered by increasing sea temperature in at least some tropical reef fishes[16,17,98,49], including coral trout[102]. Increased temperature could cause an earlier start to the breeding season in these species, and possibly a longer breeding season if thermal limits for reproduction are not exceeded.

Increased sea temperature may also impact life history traits of some reef fish species. Based on variation in life history traits of some tropical reef fishes across temperature gradients we might expect increased sea temperature to generally shift life histories towards: i) smaller maximum size, ii) reduced maximum longevity, iii) earlier maturation iv) longer breeding seasons, and v) shorter larval planktonic durations hence shorter dispersal ranges. These shifts would be observed as long-term trends in mean values for populations at any given location.

Theoretically, coral reef communities of the GBR might be expected to shift to cooler locations further south as global ocean temperatures warm. However, latitudinal expansion in coral distribution would crucially depend on a simultaneous southerly expansion of high aragonite saturation with warming waters, which is unlikely as a temperature-related increase is predicted to be much smaller than the decline due to ocean acidification[44]. Furthermore, there is a decrease in shallow water areas and an increase in siliceous sediments further from the equator, creating conditions that are less suitable for reef development. Therefore, while increased temperature may improve conditions for corals and other tropical organisms in higher latitudes, and thereby extend the range of some reef species, climate change is not expected to result in a poleward shift of coral reef ecosystems.

Increased frequency and severity of heat periods

Short-term impacts and predictions of the potential long-term impacts of an increasing frequency of heat episodes on GBR coral reefs are based on data collected during the two thermal events in 1998 and 2002, and on the present understanding of mechanisms involved in reef disturbance and recovery (Table 17.1). There are documented impacts of these events on many components of the ecosystem, including corals (Hoegh-Guldberg et al. chapter 10), seabirds and baitfish distribution



(Congdon et al. chapter 14, Kingsford and Welch chapter 18) and fleshy macroalgae (Diaz-Pulido et al. chapter 7). Changes to coral cover and available substrate following disturbance resulted in phase shifts on some reefs to an algal-dominated system.

The primary observed impact of episodic heat periods on coral reef is stress in photosynthetic organisms, coral bleaching and increased mortality of other temperature-sensitive species (chapters 5 to 16). Local diversity in reef communities is immediately reduced after heat episodes with the most sensitive species disappearing while more robust species persist or expand, such as the replacement of sensitive coral species by fleshy macroalgae that was observed after mass bleaching mortalities[55,29,79,76,122,42]. For example, most species of reef-inhabiting ascidians disappeared within two years following the 1998 ENSO event, while two bioeroding species increased significantly in numbers[64].

Further shifts in species composition result from reduced recruitment and growth rates in stressed but surviving taxa. For example, corals recovering from bleaching have up to 80 percent reduced reproductive output and growth for up to two years after the event[82,113]. During recovery, communities initially consist of sparse populations of young colonies. Depending on nutrient levels and herbivore abundances, macroalgae can proliferate and blanket space previously occupied by corals, further retarding coral recruitment and reef recovery through space occupation. Such a phase shift has been described in detail in the Caribbean, where extensive macroalgal abundances established after storms removed adult corals and overfishing and disease removed the main guilds of herbivores[41,57]. Some evidence for such phase shifts also exists for the Indo-Pacific[87].

The indirect effects of coral mortality on organism groups not directly killed by the heat episode, but dependent on the reef complex for shelter, are likely to be severe (Hutchings et al. chapter 11, Munday et al. chapter 12). The exposed skeletons of corals that die after bleaching are colonised almost immediately by benthic algae and other pioneer colonisers, and in a short period, start eroding, with three main consequences. First, coral reefs shift from a state of net calcification to erosion, less able to withstand exposure to storm waves. Second, coral recruitment is inhibited. Third, habitat is lost for the numerous invertebrates and reef fishes that are associated with corals[88,117]. For example, fish abundance and biodiversity can decline severely in parallel with declining coral cover[69]. In one case from Papua New Guinea, more than 75 percent of reef fish species declined in abundance after loss of coral cover post-bleaching, with half declining to less than 50 percent of original abundance, and importantly, several rare species became locally extinct[63]. Munday[84] also demonstrated the local (and possibly global) extinction of a specialist species of coral-inhabiting fish (goby). This study suggested that overall, habitat specialists are more likely to be prone to extinction than generalists, because of their dependence on specific habitat, and because of restricted population size and limited spatial distribution.

A major mechanism for declines in fish abundance appears to be the loss of living coral as recruitment sites for juvenile fish. Research by Jones et al.[63] suggests that marine reserves will not always be sufficient to protect fish populations if coral mortality is not prevented. Similarly, abundances and species richness in reef fish species declined after the loss of coral cover and structural complexity from coral bleaching[124]. In a study from the Seychelles, Wilson et al.[124] reported abundance in six species as 'critically low', and the local extinction of four species of fish appeared likely. Small fish species had the highest probability of decline, possibly due to their dependence on coral for food and shelter, increased competition over the remaining space, increased susceptibility to predation, and because many reef fish species require complex coral framework to recruit from the plankton.

Reef fish contribute to maintaining a wide range of ecological functions in coral reefs, and changes in their abundance can have long-term implications on ecological processes. For example, many zooplankton feeding and herbivorous fish depend on the reef framework for shelter. Zooplankton feeding fishes contribute to the capture of pelagic nutrients and pass them through excretion into benthic communities[46]. Herbivorous fish species play an essential role in controlling macroalgal abundances. Herbivores often increase in abundance following a loss of coral cover[124], presumably because more area becomes available for algal growth following coral bleaching, however, even these species ultimately decline as habitat structure is lost[103,38]. Therefore, the concern is that as the reef structure is lost, an ultimate decrease in abundance of herbivores will result in less control of proliferating algae and delayed recovery.

Other examples of cross-benefits are the excretions of damselfish, *Dascyllus marginatus*, which enhance growth and reproduction in their host coral *Stylophora pistillata*[73]. Crabs of the genus *Tetralina*, which inhabit the bleaching sensitive corals *Acropora* and *Pocillopora*, also protect their host against sedimentation[112]. Both *Tetralina* and *Dascyllus* only inhabit living corals, so their habitat is locally lost with the death of their host corals. However, for most coral-associated species that disappear when the host dies, functional roles are poorly understood and consequences of their disappearance cannot be predicted.

In conclusion, it appears inevitable that coral reef communities will change profoundly in response to rising mean annual sea temperature and episodic heat events. This change will involve a loss of biodiversity, declining ecosystem functions and services such as reef fishery yields, and a reduced aesthetic appeal for tourists. Based on present trajectories it appears almost certain that the GBR will experience a significant reduction in diversity, with sensitive species becoming rare or disappearing if no refuges exist. Some robust species that can tolerate or even benefit from higher temperatures will proliferate and gain competitive dominance over others. Overall, the potential and observed impacts of ongoing warming and episodic heat events is likely to be a substantial simplification of structural and ecological complexity, a shift from coral to algal dominance, accelerated erosion, reduced abundances or loss of temperature sensitive species, and the eventual extinction of coral-associated highly specialised species with restricted distributions and small population sizes.

17.2.2 Irradiance

17.2.2.1 Exposure

Irradiance (both visible light and ultraviolet (UV) light) is a key environmental factor for coral reefs. Coral reefs need sufficient irradiance for photosynthesis, and are therefore restricted to the upper 50 metres depth in clear oceanic waters, and four metres in turbid inshore waters[128]. However, too high levels of irradiance during hot periods can cause permanent physiological and structural damage to photosynthetic symbiotic organisms through photoinhibition and other stress processes.

Irradiance varies naturally by two to three orders of magnitude in coral reefs, at scales ranging from centimetres to whole reefs[3]. The main factors determining variability are time, local shading, surface orientation, depth, water clarity, latitude and cloud cover (Table 17.2). Globally, mean annual irradiance is greatest in shallow and clear waters of arid equatorial regions where sun inclination is steep and cloud formation is rare. On the GBR, exposure is greatest in shallow clear offshore waters, decreasing with depth and towards the coast as suspended particles backscatter a large proportion of solar irradiance on turbid inshore reefs. Latitudinal differences in irradiance on the GBR involve sun inclination angle and cloud cover, both of which are greater in the northern than the southern GBR (Lough chapter 2).

Irradiance can be affected by climate change through two mechanisms. Firstly, climate change can alter weather patterns and hence cloud cover. Cloud cover is reduced during droughts, but can also increase due to greater evaporation from warm sea surfaces. Changing weather patterns may also alter the frequency of drought-breaking floods, leading to terrestrial runoff of sediments and nutrients into the oceans that can reduce water clarity at regional scales up to several weeks[4].

Table 17.2 *Factors that affect the exposure of coral reefs to changes in irradiance, and direct or proxy measures*

Factors determining exposure	Factors determining sensitivity	Potential and observed impacts
• Water depth • Turbidity • Latitude (sun inclination) • Cloud cover • Surface roughness (waves) • Steepness and aspect of reef slope • Diurnal and seasonal changes	• Photosynthetic versus non-photosynthetic organisms • Symbiotic versus non-symbiotic • Pigments that absorb photosynthetic and UV radiation. • Species-specific photoacclimation • Susceptibility to, and factors that heighten photoinhibition and photodamage (eg anomalous temperatures) • Orientation and depth of sessile organisms that can't move into shade	• Damage to photosystem, damage to DNA • Increased mortality, reduced reproduction and growth • Shift between phototrophy and mixotrophy/ heterotrophy • Breakdown of symbiosis

17.2.2.2 Sensitivity

The photophysiology of corals, and their sensitivity to altered irradiance, is reviewed in detail in chapter 10 (Hoegh-Guldberg et al.). For most photosynthetic organisms on coral reefs, a moderate dose of irradiance, which reaches but not greatly exceeds saturation irradiance for several hours a day, should provide ideal conditions for growth. Extremely high levels of visible light and ultraviolet radiation can stress or permanently damage both photosynthetic and non-photosynthetic organisms, disrupting photosynthesis and damaging protein, DNA and symbiosis. While mobile organisms can move into shade to avoid damaging irradiance, sessile organisms that grow on upper surfaces in shallow water incorporate pigments such as mycosporine-like amino acids to protect against damage by ultraviolet radiation[26]. For photosynthetic organisms such as corals and benthic algae, extreme levels of photosynthetically active radiation can lead to photoinhibition and damage to

the photosynthetic apparatus, reducing productivity, growth and reproduction[36]. Too low irradiance doses can also cause stress, by impeding photosynthetic carbon acquisition and therefore growth and reproduction[4].

Within limits, corals can compensate for changes in exposure to light by photoacclimation, greatly widening the environmental niche where species can grow[2]. The sensitivity of corals to altered irradiance therefore greatly depends on their species-specific ability for photoacclimation. For species with poor photoacclimation, prolonged shading from thick cloud cover or turbidity can reduce primary production and growth rates as light for photosynthesis becomes limiting (Hoegh-Guldberg et al. chapter 10).

17.2.2.3 Potential and observed impacts

The entire GBR ecosystem is unlikely to be fundamentally altered by changing irradiance from climate change, as the fluctuation in irradiance is naturally high and no increasing UV trend has been observed. However, strongly reduced irradiance for a prolonged period of time, such as resulting from prolonged turbidity, can lead to mortality in photosynthetic organisms growing in deep water at the lower limit of their depth distribution[4]. Strongly enhanced irradiance for a prolonged period can also be fatal through initiation of DNA damage and of solar heat stress in very shallow and intertidal water. For example, local extinctions from heat exposure at intertidal sites in California can be predicted from the timing of low tides in summer, with low tides at noon leading to maximum solar heating[48].

The greatest impact of high irradiance is probably found during hot periods. This is because high photosynthetically active irradiance and ultraviolet radiation can exacerbate temperature-induced damage to symbiotic photosystems[62,54,71,72]. On the reef, large-scale thermal stress events, usually with periods of high irradiance and low winds[41,12,109], result in minimal waves, reduced shading by clouds, and reduced backscatter after particles settled. Such conditions lead not only to increased photophysiological stress, but also to a warming of the sea water and of benthos surfaces, with all processes potentially contributing to inducing coral bleaching and mortality[121]. Similarly, mortality from bleaching is often greatest in corals growing in shallow water and declines with depth. However, the reverse pattern is only found due to variation in community composition, with tolerant species being found in the shallows while more sensitive corals may be found in the deeper areas of a reef[55].

17.2.3 Ocean acidification

17.2.3.1 Exposure

Over the past 720,000 years atmospheric carbon dioxide (CO_2) concentrations have varied between 180 to 300 parts per million. Human activities have increased the atmospheric CO_2 concentration from 280 parts per million before the industrial revolution to 378 parts per million in 2005[106], with further increases up to 540 to 970 parts per million projected for 2100 if no drastic mitigation action occurs[59,47]. This increase in oceanic CO_2 has already resulted in a reduction of oceanic pH by an estimated 0.1 units[94,89] and of aragonite supersaturation from 4.6 to 4.0[65]. Depending on the CO_2 emission scenario used, further increases in CO_2 are expected to lower oceanic pH by 0.3 to 0.5 units over the next 100 years, and 0.3 to 1.4 units over the next 300 years[94]. As CO_2 increases and pH declines in the oceans, the ocean carbonate system also changes to lower aragonite supersaturation, possibly as low as 2.8 by the year 2100[65]. This has important implications for calcifying organisms such as corals, molluscs, coccolithophores and foraminifera that rely on carbonate supersaturation to form their carbonate skeletons (Table 17.3).

Coral records have shown that at Flinders Reef in the Coral Sea, oceanic pH has fluctuated with a periodicity of 55 years over the last 300 years, coinciding with the Pacific Decadal Oscillation[89]. However, the current and projected rate of CO_2 increase is about 100 times faster than has occurred over the past 720,000 years, that is, human greenhouse gas emissions are rapidly changing ocean chemistry to a level outside the range experienced by present-day coral reef habitats, and what most marine calcifying species have experienced throughout the past 55 million or possibly hundreds of million of years[97,94,47].

The distribution of excess CO_2 in the oceans has not been spatially uniform; carbonate supersaturation levels are highest in the tropics and decline to lower levels towards the temperate zone and areas of upwelling[97]. Aragonite saturation levels will however decline fastest in areas of highest supersaturation. The CO_2 related decline in supersaturation is far greater than the increases due to reduced solubility at warming temperatures.

***Table 17.3** Factors that affect the exposure of coral reefs to ocean acidification, and direct or proxy measures*

Factors determining exposure	Factors determining sensitivity	Potential and observed impacts
• Atmospheric CO_2 • Latitude • Temperature (small effect on solubility of key ion species)	• Calcium carbonate skeleton • Rates of physical and biological erosion and dissolution	• Less biotic and abiotic calcification, shift from calcification to erosion • Reduced linear extension ('growth') and skeletal density (stability) in calcifying organisms • Increased primary production (some plankton species due to high availability of CO_2)

17.2.3.2 Sensitivity

Globally, coral reefs built of calcium carbonate can only be found in waters where carbonate ion concentrations are above 200 micromol per kg[65]. Evidence is strong that a reduction in pH following rising CO_2 will cause profound changes in the physiology of marine calcifying organisms and in reef processes. Direct effects will be greatest for calcifying algae such as crustose coralline algae and *Halimeda*, and calcifying invertebrates such as corals and foraminifera[94,51]. The sensitivities of calcifying and non-calcifying organisms to ocean acidification are described in detail in chapters 5 to 16.

17.2.3.3 Potential and observed impacts

Some researchers have concluded that ultimately changes in ocean chemistry may have greater implications for many marine species than warming temperatures[47]. With atmospheric CO_2 rising, calcifying organisms of the GBR will be exposed to declining carbonate ion saturation state and seawater pH[94]. The full consequences of such dramatic and ongoing change in ocean chemistry are still unknown. Experiments have shown that a doubling of CO_2 partial pressure compared with pre-industrial CO_2 levels reduces calcification rates (the product of skeletal density and linear extension) in corals and coralline red algae by 10 to 40 percent[34]. A three-month experimental reduction in pH by 0.7 units was found to lower metabolic rates and growth in mussels[81] possibly from reduced rates of shell formation. An elevation of atmospheric CO_2 by 200 parts per million over six months, which lowered pH by 0.03 units, reduced both growth and survivorship in gastropods and sea urchins[108].

The physiology of non-calcifying organisms can also be modified by exposure to elevated CO_2 and reduced pH. However effects appear to vary substantially between groups, and limited studies exist in which CO_2 was realistically manipulated over longer periods, therefore longer-term effects and differences in sensitivity remain poorly understood. For example, short-term experimental CO_2 elevation resulted in reduced protein synthesis and ion exchange in some invertebrates, but not in the species of fish tested (reviewed in Pörtner and Langenbuch[91]). Importantly, non-calcifying marine plants are unlikely to be affected by increased CO_2, as most marine plants (except seagrasses) are considered carbon-saturated[39]. Little information exists on the effects of changing pH on fertilization and the survival and development of larvae and propagules, and other early life history stages in any one species.

Although fluctuations in oceanic pH, recorded at Flinders Reef throughout the last 300 years were unrelated to coral calcification rates, it is predicted that future changes in pH will be outside the range that coral reefs have experienced in modern times[89] and that ecosystem calcification will decrease while carbonate dissolution will increase[65,94]. Rising atmospheric CO_2 will therefore lead to dramatically reduced net calcium carbonate production compared with pre-industrial times, and severely weaken the ability of GBR coral reef habitats to support live coral and carbonate structures against the forces of physical and biological erosion and dissolution[67].

Presently, saturation levels are highest in the far northern GBR. By 2040, saturation levels are estimated to be 'marginal' throughout the GBR and by 2100 to be 'low' in the northern GBR and 'extremely low' in the southern GBR[67]. Aragonite saturation levels and pH will therefore drop below levels that are considered critical for calcification first in the southern GBR, preventing a latitudinal displacement of species towards cooler southern waters in response to ocean warming. These changes must be considered in conjunction with changes in sea temperature and other aspects such as the frequency and intensity of heat periods – the combined effects may well be greater than the sum of the parts. The flow-on effects of collapsed reef structures, when erosion exceeds calcification, on populations of fish and other coral-associated organisms that rely on the reef habitat are discussed in section 17.2.1.3.

17.2.4 Tropical storms

17.2.4.1 Exposure

Coral reefs of the GBR are periodically exposed to highly destructive tropical cyclones during the summer monsoon season. The total amount of energy dissipation and monetary damage of structures above water increases as the cube of a storm's wind velocity (ie a doubling in maximum sustained wind speed results in an eight-fold increase in repair costs), with the diameter and transition time of the storm additionally contributing to determine its hazard[28]. Cyclonic winds can also damage structures under water, through energy dispersed by waves, swell and surges. This section will assess the direct damage to coral reefs from storm waves (Table 17.4). The following section will cover the indirect effects from cyclone-related exposure to floods and sediment runoff from land.

Spatially, tropical cyclone activity is highest between latitudes 16 to 20 °S, with activity declining to low levels south of 22° latitude, and extremely few occurring north of 12° latitude[92] (Lough chapter 2). Even so, almost all reefs of the GBR have been affected by at least one tropical cyclone within the last 30 years[92]. Exposure also differs across the continental shelf, around reefs and with depth.

Table 17.4 *Factors that affect the exposure of coral reefs to changes in storm frequency, and direct or proxy measures*

Factors determining exposure	Factors determining sensitivity	Potential and observed impacts
• Latitude • Cross-shelf position (exposure to open Pacific swell versus shelter behind outer reefs) • Depth • Reef aspect (windward versus leeward side)	• Mobility and territoriality in fish and invertebrates • Growth forms – sessile organisms (encrusting or massive versus fragile or slender) • Low aragonite saturation and high nutrient concentrations reducing skeletal density and substratum stability of corals • Extent of bioerosion occurring in community • Cross-shelf position (more fragile growth forms inshore) • Coral community type	• Increased coral mortality, lower coral cover and diversity • Removal and redistribution of accrued calcium carbonate structure • Greatly reduced structural complexity (smaller colonies, fewer fragile growth forms) • Increased availability of substratum for algae and other pioneers after destruction of living benthos • Less shelter for coral-associated organisms • Fewer coral dwelling fish and other organisms (reduced biodiversity) • Shift in species composition towards taxa that are less affected by the outcomes of storms

Windward sides on offshore reefs at the outer edge of the continental shelf are impacted by unabated swells from the open Pacific Ocean, while leeward sides on inshore reefs are the most sheltered locations. For example, outer reefs experienced 'phenomenal' wave heights (up to 15 metres), while waves on inshore reefs and along the coast were about five metres during Cyclone Ingrid in 2005 (predictions by the Bureau of Meteorology). As the depth of wave energy is a direct function of wave height, this cyclone damaged offshore reefs down to 20 metres and deeper, whereas damage on inshore reefs was restricted to less than five metres depth (K. Fabricius unpublished data).

Consensus appears to be emerging from predictive models that the intensity and maximum wind speeds of tropical cyclones is likely to increase with rising sea temperature, while the frequency of cyclones will remain unaltered[68,118,56]. The unprecedented number of severe hurricanes in the USA and the severity of three cyclones on the GBR in the summers of 2005 and 2006 have been attributed to unusually warm sea temperatures[28,120]. It is therefore possible that severe category 4 and 5 tropical cyclones may become more common on the GBR, further increasing the degree of disturbance of coral reefs.

17.2.4.2 Sensitivity

Susceptibility to tropical cyclone damage varies widely between species and growth forms, and also changes across the continental shelf and with depth. In general, species with slim bases and slender branches, such as branching *Acropora* or large upright seaweeds (eg *Sargassum*), and organisms residing in shallow water are highly sensitive to cyclone damage. Whereas low growing (eg turf algae), massive or encrusting taxa (eg Porites corals) and deep water organisms have a higher survival probability[80]. Those made brittle by internal bioerosion will suffer even greater damage by storm erosion. On sheltered inshore reefs, branching corals tend to have lower skeletal density, more slender growth forms and more internal macro-bioeroders than their offshore counterparts that are adapted to frequent storm swells. Substratum on inshore reefs is also far weaker than on offshore reefs, due to low calcium carbonate precipitation and low abundance of crustose coralline algae (0.2% cover inshore, compared with greater than 35% on offshore reefs of the GBR[32]). Difference in substratum strength determines how susceptible massive corals are to wave damage, as massive colonies are dislodged rather than broken by waves[80]. Obviously, the combined effects of ocean acidification, nutrient enrichment from terrestrial runoff and storm damage on reef growth and complexity are likely to be far greater than the effects of each of these factors individually.

Populations of fishes, especially juvenile and sub-adult fishes, may also experience mortality and displacement, although some larger and non-territorial fish move into deeper water to avoid storm waves[70]. A large proportion of fishes and other mobile fauna later decline in abundances through the loss of habitat and shelter[124].

17.2.4.3 Potential and observed impact

The main effects of storm waves on coral reefs have been categorized as: i) coral breakage, ii) coral colony dislodgement, iii) tearing of octocorals, iv) removal of reef matrix, v) burial of organisms by shifted sediments and rubble, vi) scarring of colonies by projectiles, vii) removal of algae on inshore reefs, and viii) algal blooms[22]. Reefs in the path of severe (slow-moving category 4 or 5) tropical cyclones can lose all but the most robust organisms down to more than 20 metres depth. Reef structure is flattened, and coral skeletons are often shifted into large piles or carpets of rubble, which are unsuitable as settlement substratum for new corals until consolidation. On offshore reefs, rubble is cemented together by calcium carbonate ($CaCO_3$) precipitation, and waves remove remaining loose pieces within a few years. On inshore reefs in contrast, rubble fields may remain unconsolidated for more than 10 years. Reef recovery from extreme category 4 and 5 cyclones is slow, because few colonies survive on site to serve as brood stock to recolonise denuded areas. Recovery times may be 20 years or more for severely damaged reefs, depending on connectivity to larval sources further upstream, and the survival rate of loose fragments. Occasionally, reefs that were stressed through other forms of disturbance (eg overfishing or poor water quality) have undergone a phase shift after being hit by a cyclone, developing a new and apparently stable state of algal dominance after corals had been removed by the storm[57,96].

Less extreme cyclones cause more patchy damage, with mosaics of damaged and unbroken patches side by side, and substratum complexity remaining relatively high. Such moderate damage sets back species that may otherwise start monopolising space, and hence may contribute to maintaining high diversity on coral reefs[90]. Unlike corals surviving temperature stress (with low reproductive output up to two years after the event), unbroken cyclone survivors produce a normal amount of gametes that will recolonise impacted areas in the following years unless there is no available substrate due to increased algal cover. The speed of recovery from tropical cyclones therefore depends crucially on cyclone intensity and its speed of passage, influencing the proportion of colonies that survive and the three-dimensional substratum complexity.

Populations of non-calcifying fleshy macroalgae such as *Sargassum* can also be reduced by cyclones if holdfasts are torn off the substratum[95]. Loosely attached ephemeral algae are easily removed, but their propagules may rapidly colonise the available space after coral mortality[27,124].

Disturbance by severe tropical cyclones, which reduces habitat complexity, has been found to immediately impact fishes from all trophic levels (but especially small fishes) more severely than disturbance by coral bleaching and by outbreaks of the coral-eating starfish *Acanthaster planci*, which kill corals but leave structural complexity intact. However, after skeletal erosion of dead coral colonies, the long-term consequences of coral loss through coral bleaching and crown-of-thorn starfish outbreaks may be much more substantial than the short-term effects currently documented.

As the total energy dissipation in storms increases as a cube of wind speed[28], a potential increase in the intensity of cyclones would have profound negative implications for coral reefs. Coral cover, substratum complexity and abundances of species that are slow colonisers would all decline. Fish stock and abundance of macro invertebrates that depend on corals would also decline, while algal cover would increase (see section 17.2.1.3).

17.2.5 Rainfall patterns and river flood plumes

17.2.5.1 Exposure

Nutrient concentrations are critical for healthy coral reefs, as most reefs are adjusted to growing in low-nutrient environments through efficient nutrient recycling within and between organisms. Changing weather patterns through climate change, with more frequent droughts and more

severe floods may significantly increase the amount of terrestrial runoff into the GBR, with profound ecological consequences.

Terrestrial runoff through river flood plumes discharges large amounts of nutrients, sediments and freshwater into the GBR lagoon. Due to the predominantly southeasterly winds and northward moving inshore currents, flood plumes tend to spread northward along the coast, constituting the most important source of new nutrients to the GBR lagoon[37]. The amount, characteristics and physical transport processes of this newly imported material vary spatially, depending on rainfall, soil and slope properties, and land use. Flood plumes regularly inundate some of the nearshore reefs, occasionally reaching some of the mid-shelf reefs but rarely reaching offshore reefs of the GBR[19]. Altered climate and rainfall regimes would, therefore, predominantly affect the exposure of some inshore reefs to freshwater, sediments and nutrients from terrestrial runoff, with the severity and frequency of exposure depending on their location relative to rivers (Table 17.5) and could increase the frequency of flood-born impacts on mid-shelf reefs.

Extreme flood events are either associated with low-pressure systems during the summer monsoon or tropical cyclones (see section 17.2.4). It is unclear from present model projections whether rainfall will, on average, increase or decrease in northeast Queensland with further climate change (Lough chapter 2). The magnitude of droughts and high intensity rainfall events are likely to be greater in a warmer world[106] compared to current climate conditions with consequent effects on river flow and

Table 17.5 *Factors that affect the exposure of coral reefs to changes in rainfall and river flood frequency, and direct or proxy measures*

Exposure	Factors determining sensitivity	Potential and observed impacts
Spatial factors: • Cross-shelf position • Distance to river • Wind direction and strength during plume • Rainfall over the catchment (wet tropics versus dry tropics) • Depth • Reef morphology (gradual versus steep slopes, semi-enclosed bays versus well-flushed channels). • Extent of drought conditions between rainfall and flood events	• Species specific and life-stage specific tolerance of low salinity, low or variable light, high sedimentation, pollutants (recruits versus adults) • Nutritional strategy (phototrophy versus heterotrophy, filter feeding internal bioeroders, planktonic larvae, etc) • Nutrient limitation	• Increases in nutrients and sediments, leading to trophic shifts from phototrophy to heterotrophy; promotion of filter feeders, bioeroders • Increased algal growth, reduced coral recruitment • Increased flood mortality events. • Reduced biodiversity, altered coral community composition • More frequent outbreaks of crown-of-thorns starfish
Measures of exposure: • Salinity • Sedimentation • Nutrients • Other pollutants (agrochemicals, etc)		

the spatial extent of flood plumes affecting the GBR. Southeast Queensland is predicted to become dryer, with fewer days of cloud cover and more frequent droughts, potentially affecting the runoff pattern in the southern GBR from the Burnett and Fitzroy Rivers. As in the northeast, most models predict more intense rainfall between long periods of drought. The interaction of these two factors is important as catchments that lose grass or tree cover during periods of drought (and more frequent bush fires) will deliver more soil, soil-associated nutrients and pesticides to the GBR during intense rainfall events.

17.2.5.2 Sensitivity

The sensitivity of reef-inhabiting organisms to altered terrestrial runoff patterns, and the various components (sediments, dissolved inorganic nutrients, particulate organic matter, pesticides and light loss from turbidity) varies greatly between species, life stages, and functional groups. A review of the contrasting sensitivities of species and group is available[30] along with chapters 5 to 16 in this volume. Enrichment with dissolved inorganic nutrients and particulate organic matter, increased sedimentation and exposure to pesticides, cause a cascade of direct and indirect effects from which few ecosystem processes are spared. However, the groups most sensitive to these changes tend to be early life stages (eg coral recruits), nutrient limited phototrophs (eg some macroalgae), and nutrient-limited filter feeders (eg some internal bioeroders, some planktonic larvae). Nutrient enrichment promotes otherwise nutrient-limited groups, which then compete or prey upon other groups.

17.2.5.3 Potential and observed impacts

Extreme rainfall, resulting in large river floods, brings low salinity, sediment and nutrient-enriched waters onto coral reefs. Freshwater plumes primarily affected nearshore reefs within 20 kilometres of the coast, with extreme events resulting in freshwater on mid-shelf reefs. Fabricius[30] reviews some of the main impacts of changing water quality on inshore coral reefs. The most serious effects of enhanced exposure to materials from terrestrial runoff are reduced rates of reproduction and growth in corals and improved conditions for internal macro-bioeroders and other heterotrophic organisms. Growth of some benthic turf and fleshy macroalgae can be promoted, leading to a shift in species composition on reefs from coral to algal dominance. In contrast, most crustose coralline algae are highly sensitive to sedimentation, and may disappear in areas exposed to terrestrial runoff, having implications for coral recruits that settle on them. More turbid waters, with less structural complexity, are also associated with lower abundances of herbivorous larger fishes, possibly also releasing macroalgal abundances on the GBR[126].

Lastly, drought-breaking floods have been associated with the initiation of primary outbreaks of the coral eating crown-of-thorns starfish, possibly because the planktonic larvae depend on high abundances of large phytoplankton for their development, and such phytoplankton is most abundant in nutrient-rich conditions[9,11]. Once primary starfish outbreaks have been initiated, outbreaks can spread to reefs far away from terrestrial runoff. Therefore, terrestrial runoff affects not only some inshore reefs but can also have severe effects on remote offshore reefs[11]. Overall, reefs frequently exposed to terrestrial runoff have a lower level of resilience (lower coral recruitment, more algae and greater internal bioerosion) compared to reefs not exposed to frequent runoff. This has important implications for reefs exposed to more frequent disturbance from climate-related changes such as coral bleaching and more intense storms.

17.3 Adaptive capacity

While there is considerable information regarding how coral communities may respond to the projected changes, little is known as to how coral reefs as habitats will adapt to these changes. It is important to understand that *adaptation* in this context is not the same as *biological adaptation*, which pertains to the influence of natural selection on the genotypes within a population (evolution). This is important as evolutionary processes take considerable time and are generally not fast enough to keep pace with the speed of changes envisaged under current climate projections. In this respect, *adaptation* entails processes such as physiological acclimation (phenotypic change) and shifts in community composition over time.

Chapter 10 (Hoegh-Guldberg et al.) reviews the extent to which coral communities are likely to adapt to climate change. These responses will occur over a range of different time scales and involve a degree of uncertainty in the direction and degree of adaptation possible. At the coral reef habitat level, adaptation will be expressed as a shift to hardier species, a shift toward certain functional groups or a phase shift to algal dominance. Disturbances will selectively eliminate sensitive species; more tolerant taxa will become dominant in the community so at the community-level there is a decrease in short-term sensitivity. This effect is location-dependent and will be difficult to quantify as little is known about the sensitivity of many species living on coral reefs. Understanding these shifts will also require greater knowledge of interdependencies. Work on fish populations is providing some important illustrations of how changes in one component (coral cover) can have major impacts on other components. Wilson et al.[124] reviewed and analysed studies that documented the effects of the loss of coral on coral reef fish communities at many sites across the globe. They found that 62 percent of fish species declined in abundance within three years of disturbances that resulted in a greater than 10 percent decline in coral cover. Abundances of species reliant on live coral for food and shelter were the most consistently affected, while some of the other species, such as those that fed on invertebrates, algae and/or detrital food sources actually increased in the short-term. These types of shifts in fish communities are assessed in chapter 12 (Munday et al.).

While global extinctions are unlikely in most species due to the size of distributions, local extinctions are probable as coral reefs decline. Some coral-dependent rare endemic species with small ranges however, could be at risk of global extinction, as specific reef features are critical to reproductive success (eg coral dwelling gobies[84]). These and other issues will need greater investigation before the extent to which the current rapid climate changes will drive extinctions in tropical marine ecosystems can be fully understood.

An eventual increase in the temperature tolerance of coral reef species through genetic adaptation is conceivable, but the time frame involved in such biological adaptation is most certainly too slow to keep up with the present and projected speed of climate change. Arguments supporting the concept of adaptation to higher temperatures are largely based on the spatial differences in temperature tolerances of reef species. For example, there is higher temperature tolerance in far northern GBR corals compared with southern corals, and in corals on intertidal reef flats that were previously exposed to bleaching-inducing levels of irradiance. In contrast, presently there is no mechanism known how calcifying organisms would adapt to low carbonate ion concentrations in the ocean. Throughout geological times, rates of calcium carbonate precipitation and biotic calcification have dramatically declined when carbonate concentrations or the carbonate saturation state in the oceans lowered due to enhanced volcanic activity. Coral reefs ceased to exist for many millions of years during and after such periods, and no means of adaptation seem to have been developed throughout the evolutionary history of corals and other calcifying organisms[65]. The predicted decline in carbonate ion concentrations to levels below 200 micromol per kg might represent an even greater threat to coral reefs in the medium to longer term than increases in sea temperature. This conclusion must be tempered with the observation that a 2°C rise in sea temperature over the next hundred years.

The loss of reef structure as atmospheric CO_2 concentrations approach 450 to 500 parts per million is a major constraint to adaptation. If the ability of reef calcifying organisms to deposit calcium carbonate dwindles to zero, then reef erosion will dominate, and species and communities that are dependent on the structural complexity of coral reefs will rapidly change. Reefs will be dominated by earlier successional stages of turf or macroalgae, lower coral cover, more robust species and lower diversity. In some sense, this would be an adaptive step as the ecosystem will be less disturbed at the same level of exposure, however it would represent a new and ecologically simpler community, and its splendor and value for activities such as fishing and tourism would certainly be dramatically lowered.

The adaptive capacity at the ecosystem level will mainly be limited to shifts in community structure. Given that the rate of climate change is perhaps two orders of magnitude faster than shifts seen after the last ice age, it is not expected that genetic evolution will keep pace with greenhouse forced climate change. The second highly important characteristic of global climate change is that the earth has moved away from a climate system that is stable over thousands of years to one which is changing rapidly at decadal time scales. The criteria for selection are, therefore, changing continuously, which makes it more difficult for ecosystems to adapt and presents major challenges for managing tropical marine ecosystems.

17.4 Vulnerability and thresholds

17.4.1 Future reef scenarios

A number of models have been developed to project future impacts of climate change on coral reefs, with projections ranging from shifts in coral community structure to total ecosystem collapse. Wooldridge et al.[127] modelled successional trajectories and how they are modified by climate disturbance regimes. Their models found that more heat-tolerant coral species such as massive *Porites* are differentially favoured over heat-sensitive species such as *Acropora*; however the prevention of macroalgal dominance in free space, by protection of herbivores and of water quality, determined whether or not there was a reasonable probability that viable hard coral populations would persist beyond 2050. The study clearly showed the essential role management actions can play in enhancing the resilience of reefs at a time of increasing disturbance frequency.

Johnson et al.[61] simulated the effects on reefs of bleaching events (like that in 1998) occurring once per decade on the GBR 200 years into the future. The model predicted significantly degraded reefs by 2100, with approximately 75 percent cover of turf and coralline algae and 25 percent coral cover with decadal bleaching but no further warming. With further warming at 0.1°C per decade the model predicted greater than 85 percent algae cover and less than 15 percent coral cover, while control reefs had 60 percent algal and 40 percent coral cover.

Such scenarios are relatively mild given that most projections suggest that bleaching events of the scale of 1998 will be annual events by 2050[50,107,24]. Using the lower range of scenarios, these studies indicate that communities and reef on the GBR will trend rapidly toward an algal-dominated state, resembling those in large parts of the Caribbean and Persian Gulf where benthic communities are now dominated by organisms other than corals[57,93]. The changes that will occur in the number and community composition of other reef organisms are less easily defined but are likely to be equally dramatic, due to the high dependency on healthy coral cover. The possibility of rapid evolution of thermal tolerance in reef species is unlikely and would have to match the rate of current and future climate change to maintain the current *status quo* (0.2 to 0.6°C per decade)[24].

These scenarios are also best-case scenarios given that they do not incorporate the interactive effects of other changes such as tropical cyclone intensity, sediment destabilization by drought, larger flood events and other factors, and because they do not consider adequately how ocean warming, acidification and sea level rise may interact. Currently, work that has explored how temperature and acidification interact is sparse and conclusions are surrounded by controversy (McNeil et al.[77] versus Kleypas et al.[66]). Understanding these interactions should be a priority. It is also clear that a better understanding of the implications of an increasing frequency of disturbance events like cyclones is needed. Since extreme events are rare, observational data are sparse to ground-truth models and they are more difficult to predict (and for organisms, more difficult to adapt to) than steady continual warming or less severe events.

17.4.2 Factors influencing resilience

The term *resilience* has been used widely to describe the overall ability of tropical marine ecosystems to recover from disturbances[99,23,121,58,86]. Resilience is critical for reefs to withstand the shifting and increasingly hostile conditions of tropical waters under climate change, and an essential factor in the assessment of vulnerability.

The resilience of reefs is inextricably linked to factors that influence the growth, reproduction and survival of key functional groups on coral reefs. The assumption is that well-connected reef systems generally take 10 to 20 years to fully re-establish after a massive disturbance. For example, in the southern GBR, in a region of high connectivity with undisturbed reefs, a storm reduced coral cover from 80 to 10 percent, with consequent decline in abundances of 88 percent of fish species investigated. Both coral cover and fish abundance recovered to pre-disturbance levels within 10 years[45].

Recovery is significantly slower on more isolated atolls that are poorly connected to larval pools. Studies of reefs in northern waters of Western Australia have shown that isolated reef systems recovered more slowly after the 1998 mass coral bleaching disturbance, than mosaic reef systems[111]. Similarly, live coral was reduced by 90 percent on the inner islands of the isolated Seychelles, with no apparent depth refuge[107]. Seven years later, fleshy macroalgal cover had increased seven-fold, dominating many of the carbonate reefs. Only one percent of the benthos consisted of habitat-forming branching and plate corals, while the remaining 6.5 percent of live corals were massive and encrusting growth forms that offered limited shelter for reef-associated organisms[124]. The finding of slow coral recovery, high macroalgal abundance and low abundance of grazing herbivores raises serious doubt about the potential of remote and isolated reef systems to recover, due to their poor connectivity to larval pools, despite few other human-induced stressors[124].

Even in well-connected reef systems, longer-term trajectories for the composition of reef communities is shaped by disturbance history, as the effects of cumulative disturbances are often greater than the sum of individual disturbances[57]. Offshore reefs in the northern GBR have experienced a series of serious large-scale disturbances within the last 15 years (bleaching in 1998 and 2002, severe *A. planci* outbreaks in 1988 to 1992, and 1995 to 1998, and category 5 Cyclone Larry in 2005[114]. Such repeated large-scale disturbances destroy brood stock and physical structure of the ecosystem at regional scales, severely compromising the ability of this region to recover from climate related disturbances in the coming decades.

More chronic disturbance such as fishing pressure and changes to water quality also greatly affect the resilience of reefs. For example, the over-exploitation of fish populations that are threatened by a loss of primary habitat due to climate change will clearly hasten the loss of these fishes from coral reefs. If fish populations on coral reefs are fished too heavily, then the functions they provide (grazing, predation) will dwindle with the effect that reefs may become vulnerable to a community shift away from coral and toward macroalgal assemblages. Lessons from other coral reef areas (eg Caribbean[57]) have demonstrated the importance of complexity and diversity in maintaining the ability of coral reefs to bounce back from disturbance. The key interactions are likely to be between climate change and more local human activities, such as fishing pressure, water quality and coastal land use. These elements are critical to societal responses to a rapidly changing climate. Given that projections indicate that disturbances are likely to increase in frequency and intensity under even low range emission scenarios, the importance of resilience over the coming decades will only increase. While there must be rapid action on the core issue of reducing greenhouse gas emissions, managing coral reef habitats to increase their resilience to change is vital if we are to give them the best change of surviving rapid climate change.

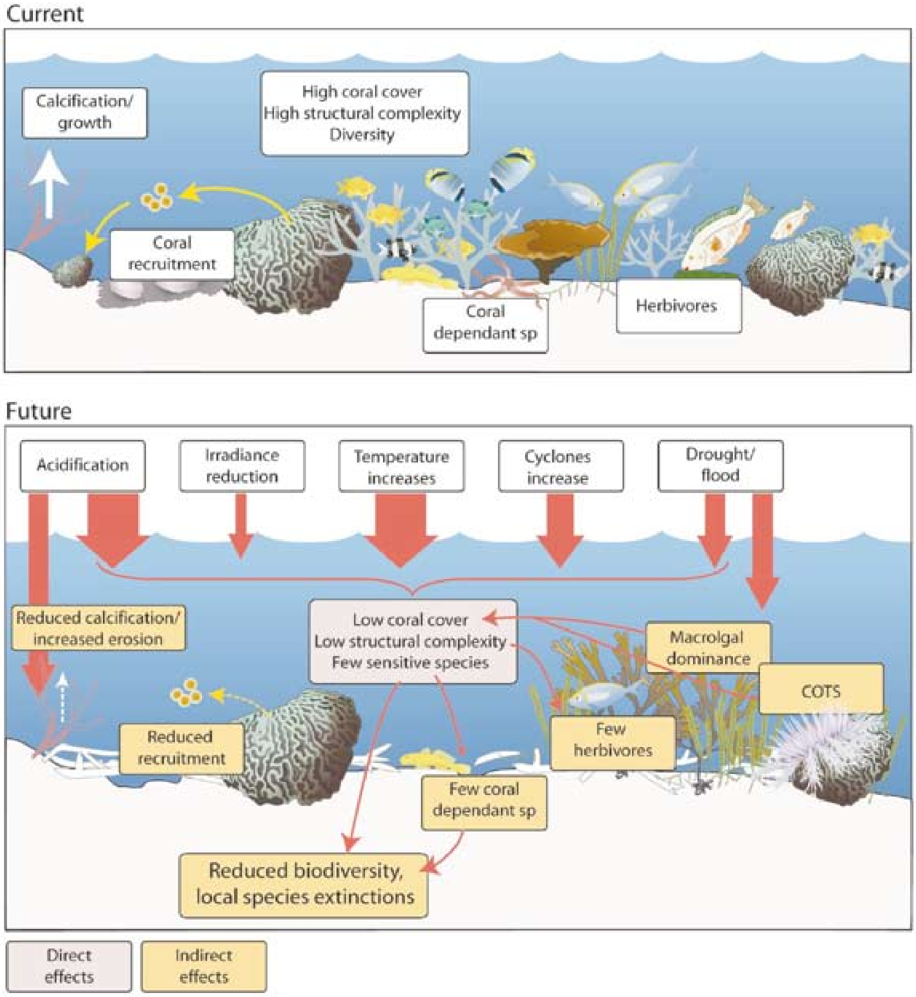
17.4.3 Vulnerability of coral reefs to climate change

Data compiled in the previous sections on the exposure, sensitivity, impacts, adaptive capacity and resilience of coral reef habitats confirm the findings from many previous studies. That the presently observed extent and rate of climate change, and the associated higher frequencies of extreme weather events, constitute a severe threat to the presence and future health of coral reefs[40,12,23,50,65,21,58,107,52]. Here we summarise in a simple conceptual diagram the expected responses of coral reefs to the five main climate change factors; temperature, irradiance, acidification, storms and floods (Figure 17.1). The diagram emphasises that some of the direct effects on reefs are common across the five main climate change variables: they all reduce coral cover, structural complexity and available habitat, and the number of sensitive species. The effects of acidification and temperature are of most concern, whereas changing irradiance is probably of least concern. These direct effects lead to flow-on effects on major ecosystem properties, including:

- Shift in balance from net calcification to net erosion.
- More bare substratum available for algae to settle, resulting in a shift from coral to algal dominance and presence of algae retarding coral recovery.
- Lower structural complexity leading to reduced habitat and shelter for fish and other coral-associated organisms.

- Local extinctions of sensitive, rare and highly specialised species; possibly some global extinctions of endemic species that are unable to migrate or compete with other species for resources.
- Reduced population sizes leading to reduced reproduction and recruitment, and longer recovery times.
- Simpler, ecologically less complex ecosystems, overall reduction in biodiversity.

Figure 17.1 *Predicted direct and indirect impacts of the five main climate change variables on coral reefs and how this will influence coral reefs in the future*[c]



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[c] Through repeated and prolonged impacts, reef communities will adapt to a state of lower sensitivity, however essential ecosystem properties such as biodiversity, reef calcification and coral dominance are lost

Additionally, each climate variable exerts certain specific direct and indirect effects on the ecosystem. For example:

- Ocean acidification reduces precipitation and enhances dissolution of carbonate.
- More frequent drought-breaking floods cause eutrophication, fostering the growth of macroalgae, filter feeders and outbreaks of coral-eating crown-of-thorns starfish.
- Higher temperatures accelerate growth in some organisms, however coral cover is reduced as bleaching thresholds are exceeded more frequently.
- Elevated sea temperatures reduce fecundity and recruitment in surviving corals.
- Warming leads to expanding or contracting geographic distributions of species that are adapted to specific temperature ranges, with unpredictable effects on species interactions.

17.4.4 Thresholds

Given the dependency of coral reef habitats on healthy coral populations, thresholds associated with change at the ecosystem level are inevitably similar to those of corals. In this regard, increases in sea temperature of more than 1°C will drive an increase in frequency and intensity of mass coral bleaching events, if no adaptation or acclimation occurs. Increasing concentrations of CO_2 will lead to a decline in pH and in carbonate ion to concentrations below 200 micromol per kg, a point at which corals will no longer calcify. As discussed above, numerous other changes will occur that will tip the balance of coral reef accretion and structure toward that typical of non-carbonate reef ecosystems. Based on this reasoning, the threshold for significant change to occur will be reached near 450 to 500 parts per million atmospheric CO_2 concentration. At this level, tropical seas will be further warmed by 1 to 2°C towards a temperature where coral mortality from bleaching will be a common event, and seawater carbonate saturation will be decreased to below 200 micromol per kg where calcification is severely reduced.

17.4.5 Assessment of spatial patterns of vulnerability to climate change

In order to identify regions in the GBR that are potentially most vulnerable to the effects of climate change, we qualitatively assessed the spatial distribution of all major potential environmental and biological predictors of vulnerability. West and Salm[121] and Salm et al.[101] identified the main physical and biological factors that contribute to bleaching outcomes, including the physical factors related to high temperature exposure, water movement, mixing and irradiance, and biological factors such as bleaching history, pre-exposure to low tides and high fish abundances as maintained through a network of protected areas. Done et al.[21] tested four of these physical and biological factors related to bleaching resistance in the GBR, using surveys late in the 2002 bleaching event. They found strong support for the effects of local warming, cooling by hydrodynamic mixing (modifying exposure and sensitivity), and sensitivity differing between four coral community types. They also found inconsistent effects of pre-exposure and relatively weak support for the role of irradiance in determining bleaching and mortality. Hoegh-Guldberg[50] concluded that the GBR will be more vulnerable in the south than in the north, due to greater sea surface temperature increases in the south (approximately 0.5°C versus approximately 0.3°C since the late 19th century, respectively; Lough chapter 2).

Berkelmans et al.[8] found that the spatial distribution of coral bleaching in the GBR in 1998 and 2002 was best explained by short-term thermal exposure (the 3-day maximum temperature around a reef) rather than longer-term median or deviations from the long-term average physical conditions. Wooldridge et al.[127] demonstrated the importance of water quality and herbivores in determining macroalgal abundance and hence the vulnerability and resilience of reefs. Skirving et al.[110] confirmed through mathematical models the important roles of low wind and currents and cloudless skies in inducing bleaching conditions. Many other studies have tested additional aspects of the potential contributions of physical and biological factors in enhancing or ameliorating hazard, and justifying their inclusion as risk factors. As a first and preliminary approach, a qualitative assessment of the distribution patterns in the spatial distribution of the potential risk and resilience factors across the GBR regions is compiled in Table 17.4 and in Figures 17.2 and 17.3.

Table 17.4a lists all of the known risk factors that may lead to an increased probability of climate impacts. Highest long-term means mostly appear to be located in the southern and central GBR, while none of the risk factors had highest values in the far northern and northern regions. For example, in the southern GBR alkalinity saturation and coral growth rates are assumed to be lowest while mean annual temperature variation and long-term warming trends are highest. Some of the risk factors are also assumed to have higher values in the inshore region compared with the offshore region, for example, long-term summer temperature averages are generally greater than 1°C warmer inshore than offshore (Lough chapter 2). Seasonal water temperature fluctuations are higher inshore due to longer water residency times on the continental shelf and distance from cool-water upwelling[125,8]. Corals on inshore reefs are also exposed to more variable irradiance from turbidity, and less swell-induced flow. They are also significantly darker than their conspecifics in cleaner offshore waters, in response to elevated particulate nutrients, nitrate and shading. All these factors may contribute to greater exposure to climate change, suggesting a potentially greater risk for inshore areas compared with offshore areas, and for the southern region compared with the far northern region of the GBR.

Table 17.4b lists the factors that are likely to contribute to reef resilience. It confirms the patterns seen in Table 17.4a of greater pressure in the southern region than in the far northern region. Again, many of the resilience factors have highest values around offshore reefs compared to inshore reefs (eg maximum cooling through upwelling and mixing from currents and swell offshore, and steeper slopes offshore than inshore).

This assessment, graphically summarised in Figures 17.2 and 17.3, suggests that at a regional scale, the far northern region, and in particular its offshore reefs, may have the most favorable spatial, biological and physical conditions within the GBR, supporting their relative greater resilience to climate change. In contrast, inshore reefs of the southern and central regions of the GBR appear to have the least favorable environmental conditions, exposing them to the greatest probability of long-term damage from climate change. However, it is very important to stress that the spatial pattern proposed here is preliminary, purely qualitative and conceptual. It will need to be rigorously tested using quantitative information and a formal risk mapping approach, to test and verify the apparent spatial patterns in the vulnerability of the main GBR regions to climate change. The relevance and relative importance of the different factors in protecting coral reefs will vary considerably spatially and temporally.

Table 17.4 *(a) Risk factors: regional conditions that increase vulnerability to climate change impacts on coral reefs in the GBR[d,e] (b) Resilience factors: regional conditions that reduce the vulnerability to climate change impacts on coral reefs in the GBR*

17.4a	Inshore	Offshore
Far Northern	Fluctuations in water clarity Macroalgal dominance after coral loss	
Northern	Moderate fishing effort Frequent crown-of-thorns starfish outbreaks Macroalgal dominance after coral loss Fluctuations in water clarity	Moderate fishing effort Frequent crown-of-thorns starfish outbreaks
Central	High cyclone frequency High sea temperature warming (approximately 0.4°C since 1903) Most frequent crown-of-thorns starfish outbreaks High fishing effort Macroalgal dominance after coral loss High exposure to terrestrial runoff Fluctuations in water clarity Reduced species richness	High cyclone frequency High sea temperature warming (approximately 0.4°C since 1903) Most frequent crown-of-thorns starfish outbreaks High fishing effort
Southern	High seasonal temperature amplitude High sea temperature warming (approximately 0.5°C since 1903) Low alkalinity super-saturation Low cloud cover Low calcification Moderate fishing effort Macroalgal dominance after coral loss Low species richness Fluctuations in water clarity (drying catchments, episodic storms that increase sediment transport)	High sea temperature warming (approximately 0.5 °C since 1903) Low alkalinity super-saturation Low cloud cover Low calcification High fishing effort Frequent crown-of-thorns starfish outbreaks Low species richness

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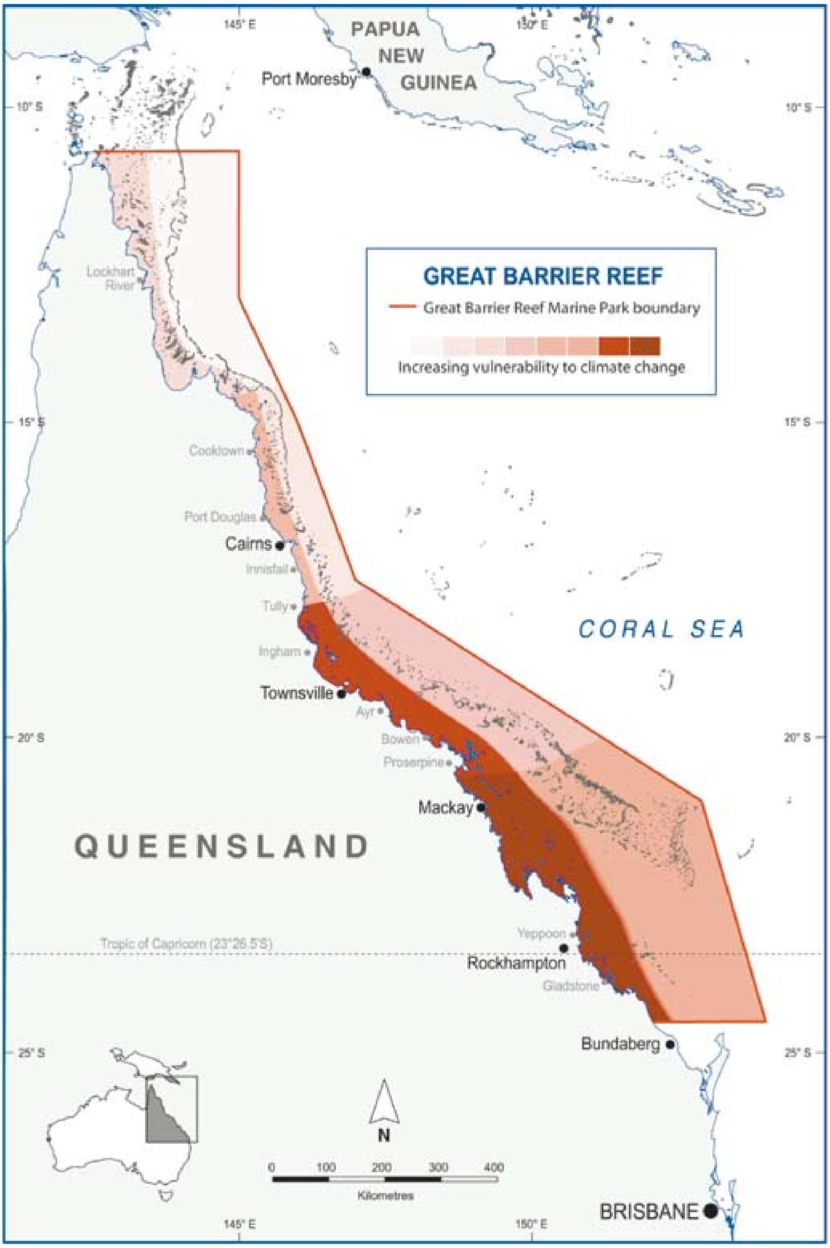
[d] The separation is based on the four GBRMPA Management regions: far northern (north of Lizard Island): 11.3° to 14.5 °S; northern (Innisfail / Mourilyan Harbour up to Lizard): 14.5° to 17.5 °S; central (north of Mackay up to Innisfail): 17.5° to 21.0 °S; and southern (south of Mackay): 21° to 24.5 °S. 'Inshore' represents the region reaching from the coast to 33 percent across the continental shelf (approximately to the outer edge of the lagoon), and 'offshore' represents from 33 percent across to the outer edge of the continental shelf where oceanic processes dominate.

[e] Fishing effort estimates are based on the Queensland Department of Primary Industries and Fishing Coastal Habitat Resource Information System data and refer to all types of fishing (commercial and recreational) on reef habitats only. Estimates do not include netting or trawling effort in inter-reef areas.

17.4b	Inshore	Offshore
Far Northern	High alkalinity super-saturation High cloud cover Low sea temperature warming (approximately 0.3°C since 1903) Low cyclone frequency Low fishing effort Few crown-of-thorns starfish outbreaks Low exposure to terrestrial runoff High coral species richness High annual mean temperature tolerance in corals	High alkalinity super-saturation High cloud cover Low sea temperature warming (approximately 0.3°C since 1903) Low cyclone frequency Low fishing effort Few crown-of-thorns starfish outbreaks Low exposure to terrestrial runoff High coral species richness High annual mean temperature tolerance in corals Low seasonal temperature amplitude Cooling through upwelling, mixing from currents and swell, shading from steep slopes Conditions less suitable for macroalgal growth
Northern		Cooling through upwelling, mixing from currents and swell, shading from steep slopes Conditions less suitable for macroalgal growth
Central		Low exposure to terrestrial runoff Cooling through upwelling, mixing from currents and swell, shading from steep slopes Conditions less suitable for macroalgal growth
Southern		Low exposure to terrestrial runoff Cooling through upwelling, mixing from currents and swell, shading from steep slopes Poor conditions for macroalgal growth

Figure 17.2 *Map of the predicted vulnerability of coral reefs of the GBR to climate change*[f]



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[f] Based on a qualitative preliminary assessment of the spatial distribution of the main climate and other environmental factors that are likely to affect the degree of risk and resilience (see Tables 17.4 a and 17.4 b). Importantly, this assessment is conceptual rather than quantitative, and there are no firm boundaries of regions, hence the shades of risk are indicative rather than quantitative

At within-reef scales, spatial differences in vulnerability appear limited. Windward and leeward sides appear to show a similar number of risk factors and resilience factors, and shallow areas have only slightly more risk factors compared to deep areas (Table 17.5 and Figure 17.3). However, sheltered and poorly flushed lagoons and embayments appear to be most exposed to risk factors, and have the lowest resilience factors with regards to bleaching, whereas well-flushed flanks are probably best protected against damage from bleaching[116]. In contrast, well-flushed areas may be the least protected against ocean acidification, as locally buffering dissolving calcium carbonate would be flushed away and unable to protect calcifying biota[20].

In summary, the spatial distribution of risk factors suggests that long-term vulnerability is greatest in inshore regions of the southern and central GBR, and in shallow waters, lagoons or bays. In contrast, resilience is highest in offshore reefs of the far northern GBR and on well-flushed flanks (Tables 17.4 and 17.5). These preliminary predictions were compared against observed bleaching patterns in the

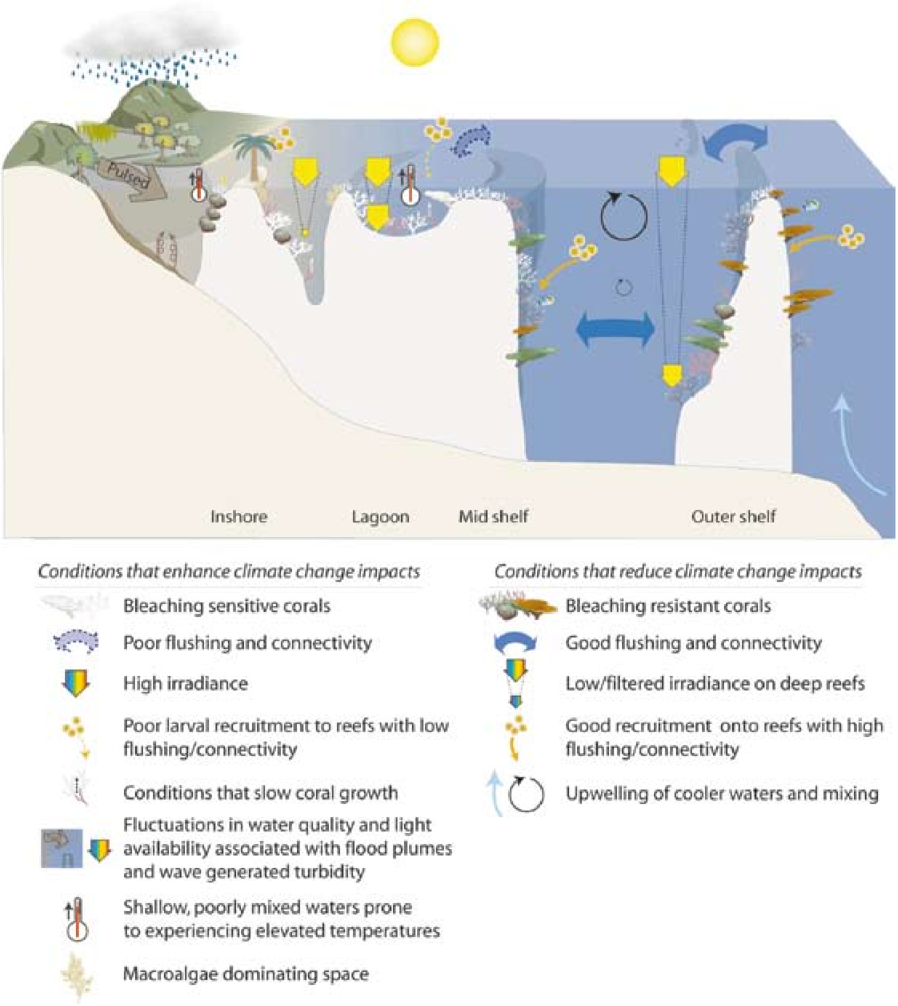
Table 17.5 *(a) Risk factors: local conditions that increase vulnerability to climate change impacts within coral reefs (b) Resilience factors: local conditions that reduce vulnerability of climate change impacts within coral reefs.*

17.5a	**Shallow**	**Deep**
Front (windward)	High irradiance Fast macroalgal growth (inshore) Sensitive communities	Slow coral growth, slow recovery Sensitive communities
Back (leeward)	High irradiance	Slow coral growth, slow recovery Sensitive communities High levels of sedimentation
Lagoon and bays	High irradiance Low flushing – high sea temperature heating Low larval settlement Slow coral growth, slow recovery	Low flushing, wave mixing – greatest sea temperature heating Low larval settlement Slow recovery (very slow coral growth) High levels of sedimentation
Flank	High irradiance	

17.5b	**Shallow**	**Deep**
Front (windward)	Fast growth Low sedimentation High wave mixing	Low irradiance
Back (leeward)	Resistant communities (inshore)	Low irradiance Poor conditions for macroalgal growth
Lagoon	Resistant communities	Resistant communities Low irradiance
Flank	High flushing Fast growth	Resistant communities Low irradiance

1998 and 2002 events. Arial surveys showed that bleaching was more severe inshore than offshore, with 74 versus 21 percent of reefs bleached in 1998, and 72 versus 41 percent in 2002[8]. Offshore reefs in the far northern and the southern (Swains complex) regions experienced little bleaching, and inshore reefs in the far northern region showed slightly less bleaching than inshore reefs in the central and southern regions. Satellite-derived 3-day maximum sea surface temperatures explained 73 percent of the variation in the occurrence of bleaching between reefs, and the odds of bleaching increased 5.7-fold with every degree increase in 3-day maximum temperatures[8]. Underwater surveys showed that bleaching damage was more severe inshore than offshore, and more severe in shallow than in deeper waters, and that less bleaching occurred in well-flushed channels than in lagoons and ponding back reefs[21]. It is obvious that a better system understanding and more quantitative data need to be considered to test and verify the preliminary predictions made here.

Figure 17.3 *Overview of some of the main physical, spatial and biological factors that affect the vulnerability of coral reefs to climate change*



17.5 Linkages with other ecosystem components

Although coral reefs represent only 6 percent of the area of the GBR Marine Park, they are vitally connected to other GBR habitats including mangroves and salt marshes, seagrass meadows and estuaries, as well as pelagic environments[15] (Sheaves et al. chapter 19). Reefs act as barriers against oceanic waves providing shelter that is critical to mangroves, seagrasses and salt marshes. Loss of connectivity, both physically and ecologically, will affect the movement of nutrients, pelagic organisms (particularly planktonic larvae and invertebrates), as well as the survival and dispersal patterns of eggs, larvae and juveniles of reef species, compromising ecosystem functions. Flow-on effects to coral reefs are to be expected as other ecosystem components are deleteriously impacted by climate change, and ecosystem diversity and functions decline.

Pelagic environments (primarily through resident plankton) directly support a wide variety of suspension feeding organisms and planktivorous fish on coral reefs. Planktivorous fish are the largest trophic category of fishes by weight and number at shallow depths on GBR coral reefs (McKinnon et al. chapter 6). Similarly, many coral species rely on plankton and suspended particulate material as a primary food resource. As primary productivity of plankton communities is affected by changes in sea temperature, rainfall patterns, runoff and ocean circulation, the transport and availability of nutrients to reefs will decline. This will in turn decrease food quality and quantity for higher trophic levels with a resultant decline in abundance and diversity of other species on reefs (Kingsford and Welch chapter 18).

Mangroves and salt marshes, seagrasses and wetlands are a complex connected mosaic of habitats that are important nursery and juvenile habitats for many coral reef species. The movement of these species result in the transfer of materials between habitats through grazing, predation, and excretion (Waycott et al. chapter 8, Lovelock and Ellison chapter 9). Material exchange between mangroves, salt marshes and seagrasses and other adjacent habitats are critical for the survival of many reef species. Therefore loss of seagrasses or mangroves, or changes in productivity, are likely to affect reef species that spend part of their life history in these habitats and may be important members of the reef trophic structure. In addition, sediment filtering and trapping, nutrient cycling and substrate stabilisation are important functions of these habitats that may be compromised by climate change (Waycott et al. chapter 8, Lovelock and Ellison chapter 9). The implications for reefs are that any increased delivery of sediment or nutrients to inshore reefs reduces water quality and threatens reef resilience and recovery after disturbance.

17.6 Recommendations

17.6.1 Potential management responses

Concerns about the status and future of coral reefs are increasing. Coral reefs are shaped by disturbance regimes, and storms and freshwater floods have exerted major influence on the ecology of coral reefs throughout millennia. However, climate change, through the rapid increase in atmospheric concentrations of greenhouse gases like carbon dioxide, is changing the rate of disturbance as well as changing baseline climate conditions. This in turn is exacerbating human related disturbances such as fishing, destructive fishing and water pollution[10]. The frequency and severity of disturbance of coral reefs is unprecedented in modern times, and several global assessments conclude that about

27 percent of the world's reefs have been damaged or destroyed, while a further 50 percent have already been severely degraded as a consequence of human activity[104,123]. Should ocean pH continue to decline while temperatures continue to rise as a result of anthropogenic greenhouse gas emissions, then reef structure will be lost as carbonate dissolution and coral bleaching continue to increase both in severity and frequency. A dramatic loss in reef biodiversity appears inevitable at atmospheric CO_2 concentrations approaching 500 parts per million. Given that impacts on many other ecosystems also become extreme at 450 to 500 parts per million, limiting emissions to below this point is critical for coral reefs.

There is little doubt that coral reefs of the GBR are particularly vulnerable to climate change. Disturbance by climate change, when combined with other existing human stressors, is likely to further degrade this valuable ecosystem, and threaten resilience. Effective management strategies to reduce the impacts of climate change and promote resilience are essential to ensure the future survival of coral reefs. It is important to understand that these management responses are not a solution to the problems faced by coral reefs under human-driven climate change. They must therefore be part of a strategy that involves stabilising atmospheric CO_2 at concentrations less than 450 to 500 parts per million. Strategies to enhance reef resilience have started to emerge[100,127], and are briefly summarised here. Unfortunately, no strategy for addressing the effects of ocean acidification on coral reefs is presently known.

To maximise the ability of the GBR to cope with climate change, the impact of other anthropogenic stresses must be reduced. The authors recommend the following management strategies should be considered as a matter of priority:

- *Protection of water quality:* Deteriorating water quality from increased runoff of sediments, nutrients and agrochemicals from agricultural land is a major anthropogenic threat to inshore coral reefs. The *Reef Water Quality Protection Plan* aims to 'halt and reverse the decline in the quality of water entering the GBR lagoon by 2013'. Continued effective implementation of this plan is considered essential to maintain the ecological balance in coral reefs, reduce disturbance from terrestrial runoff and the consequences on coral recruitment, algal abundance and frequency of crown-of-thorns starfish outbreaks[30,11].
- *Protection of coastal habitats:* The protection of coastal habitats such as mangroves and salt marshes, estuaries and seagrass meadows will maintain key functions of these habitats. Functions such as sediment filtering and trapping, nutrient cycling and substrate stabilisation are important for addressing poor water quality and reducing sediment and nutrient delivery to GBR reefs. Protecting coastal habitats will also maintain the connectivity between these habitats and coral reefs, and the critical habitat they provide for reef species that spend part of their life cycle in these habitats[15].
- *Protection of biodiversity:* A comprehensive network of adequate and representative marine areas exist in the GBR Marine Park. There is now increased biodiversity protection with 33 percent of the GBR Marine Park designated as no-take areas, and protection of inter-reef habitats from bottom trawling in other areas. This type of protection will play a role in preventing the destabilisation of ecological balance and macroalgal proliferation after corals die, and hence assist corals to recover more quickly from disturbances. Networks of marine protected areas are generally considered an essential strategy to improve reef resilience[101], and in the GBR they will play a significant role in minimising impacts from the increasing frequency of climate change related massive disturbances.

Furthermore, some interventionist approaches have been proposed recently to lessen the direct impacts of climate change on coral reefs of the GBR. The following management strategies have been discussed:

- *Shading and mixing:* Shading by clouds or steep islands reduces bleaching damage in corals[62,83,33]. Similarly, water turbulence lessens bleaching damage[85]. Trials have begun with tourism operators on the GBR to explore the utility of shading small patches of economically important reefs close to tourist pontoons to reduce the amount of damage occurring during mass bleaching episodes. Such proposed management intervention may be effective on very small scales, protecting key sites that may have economic or other significance, but it is obviously not a solution to remediate climate impacts at an ecologically relevant scale. Furthermore, the economic viability of erecting structures like shades may become more compromised should cyclone intensities increase.
- *Transplantations:* Another local scale, coral bleaching specific strategy has been proposed by some researchers to seed the southern GBR with potentially more temperature adapted genotypes of endosymbiotic dinoflagellates and corals from the northern GBR. As numerous environmental conditions differ between north and south (eg naturally lower aragonite saturation, lower winter temperatures, different types of predators, more vigorous macroalgae), the success and ecological implications of such transplantations are unknown. Such experiments have limited application while the implications for the wider ecosystem are not reliably understood or addressed. Before any trails of this nature can be conducted, comprehensive research is needed to predict the likelihood of success and to avoid potential disruptions in ecosystem functions such as the spread of coral disease.

Alleviating the rate and magnitude of climate change pressure on species and habitats of the GBR is an essential strategy. As few obvious regional-scale strategies exist, it is an ecological and economic imperative for the world population to substantially cut greenhouse gas emissions, and slow the predicted rate and extent of change in the global climate. This requires the rapid adoption and implementation of effective greenhouse gas mitigation strategies.

17.6.2 Further research

Research is urgently needed to improve the ability to predict future climate change impacts on coral reefs, and integrate both natural and climate change-related stressors in future models. The following list represents top research priorities to improve our ability to assess vulnerability and predict change. A better understanding of these questions might also facilitate the development of new management strategies, and prioritisation of potential management options:

- *Understanding adaptation:* Mechanisms and time frames of acclimation and adaptation at all levels of biological organisation, from molecular to ecosystem level. This knowledge is essential to support our capacity to predict ecosystem changes in response to climate change.
- *Identifying refuges:* Mapping the main refuges from climate change for the next 30 years. Data and models are needed to test and quantify the proposed schematic latitudinal, cross-shelf and within-reef gradients in exposure and potential impacts. These refuges will be important for maintaining and supporting reef resilience, and must be given the highest level of management protection.

- *Climate change stress interactions:* Quantify the interactive and synergistic effects of ocean warming, aragonite saturation and increased storm frequency on ecosystem calcification budgets for the different regions of the GBR.
- *Climate change and other stressors:* Quantify the specific interactions and synergies between climate related ecosystem disturbance and water quality. Quantify the specific interactions between climate related ecosystem disturbance and fishing pressure. How do poor water quality and fishing pressure affect reef resilience?
- *Life history impacts:* Investigate the influence of higher water temperatures on the life history of planktonic life stages and metamorphosis in key reef organism groups.
- *Transplantation:* Investigate the likely consequences of seeding high-temperature adapted coral gametes and zooxanthellae from the northern part of the GBR on reefs in regions further south.
- *Ocean acidification and calcification:* Quantify the specific effects of changing aragonite saturation for benthic and pelagic calcifying organisms and explore adaptive mechanisms to continue calcification at lower carbonate supersaturation.
- *Extinction risk:* What are realistic rates of local and global species extinctions in response to climate change, and what are the properties of marine species that are most at risk of extinction? What would species extinctions mean for the GBR ecosystem?
- *Ecosystem stability:* The role of species redundancy in maintaining ecosystem stability and the linkages between species diversity and specific coral reef functions.

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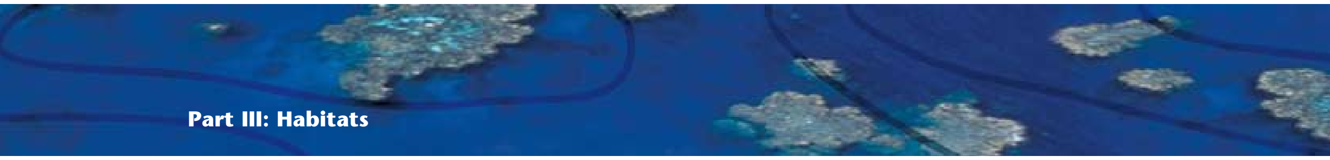

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